among larvae.

It is notable that we found an extremely high density of medusae in both the day and night samples. It is possible that the low densities of all taxa in both day and night samples relative to those found in past studies (Chiavelli et al. 1998, Pickhardt et al. 1999) could be explained by intense feeding by these medusae in the sampling location.

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Nocturnal activity and spatial distribution of the balloonfish, *Diodon holocantus*

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Abstract: Niche diversification theory may help explain the paradox of high fish diversity despite finite resources in Caribbean coral reefs. Balloonfish (*Diodon holocantus*) may be nocturnally active in order to capitalize on food resources that are predominantly available at night and/or to avoid visual predators. The various sized balloonfish may differentially distribute themselves across the reef with smaller fish being more abundant in more protective habitats. Balloonfish were found to be more active during the night than the day. Balloonfish were more abundant at night in patch reef, and more abundant during the day in the mangroves. Additionally, small balloonfish were more common in the mangrove while large and medium fish were encountered more frequently in the patch reef. The mangroves may be a refuge for small balloonfish. Different selection pressures in the mangrove as compared to the rest of the back reef may result in distinct balloonfish behavior in the two habitats.

Key Words: balloonfish, coral reef, niche diversification, pufferfish, diel patterns

Introduction

Although Caribbean coral reefs host a diverse assemblage of fish and are among the most productive ecosystems in the world, fish abundance on these reefs are limited by finite food and shelter resources (Ormond et al. 1996). Niche diversification, a theory proposed to explain this paradox of high diversity despite resource limitation, suggests that fish are temporally and spatially distributed so that each species occupies a unique place in the resource continuum. In addition to interspecific resource partitioning, species can ease intraspecific competition by spatially or temporally isolating conspecifics.

One way species may partition resources is by being active during different times of the day. The balloonfish (*Diodon holocantus*) diet is partially composed of nocturnally active prey. This, in combination with the unique morphology of balloonfish suggests that they occupy a nocturnal niche. Balloonfish are bulky with small fins that are ill-suited for high-speed predator avoidance and have the large eyes associated with nocturnal fish. During a night survey of a back reef in Jamaica, more balloonfish were observed than in similar day surveys. If balloonfish are nocturnal, then they should be more visible and more active during the night.

Balloonfish may distribute themselves differentially across the reef, both according to their preferred habitats and to size class. Initial surveys suggested disproportionately high abundance of small balloonfish in the mangroves adjacent to the reef, as compared to other reef zones. If balloonfish distribute themselves across the backreef according to size, than more small balloonfish should be found in the mangroves, which may offer protection from predators, and more large balloonfish in the patch reef, sand, and grass habitats, places which may have more food but also more predators.

Methods

In order to investigate our two hypotheses, we first evaluated differential distribution of balloonfish across the reef, and then nocturnal activity. From 9:30-11:00 and 21:30-13:00 on 6-8 March 2000, we searched for balloonfish on the backreef of Discovery Bay, Jamaica (total search hrs = 15.8). We surveyed each of three zones (patch reef, sand, and grass) for approximately 1 h each day and night. The mangroves just SW of the Laboratory, a fourth zone, were surveyed during an additional 20 min each day and night (time required to search the entire grove). The reef crest and forereef were also initially surveyed during the day, but excluded from consideration when we found very few balloonfish in these habitats. For each balloonfish encountered, its size class (< 10 cm = small, 10 - 17 cm = medium, > 17 cm = large), activity (swimming, resting), habitat (patch reef, grass, sand, mangrove), and crypsis (hidden, exposed) were recorded. We used a goodness of fit test to assess the effect of size class distribution across different reef zones. A two-way ANOVA was used to test for the interactive effects of time of day and reef zone on the number of balloonfish found per min. Linear, orthogonal contrasts were then used to compare day and night balloonfish abundance within each zone.

On 9 March 2000, individual balloonfish were observed for 5-15 min intervals (11 by day, 9 by night). At night, fish were identified by white light and then observed by red light. Fish activity was recorded every 30 s. The proportion of time spent active (swimming or foraging) was calculated for each fish. As these proportions were not homoskedastic, a Wilcoxon test was used to analyze the effect of time of day on fish activity. We used a goodness of fit test on our original survey data to also assess the effect of time of day on activity (resting or swimming).

Results

The pooled day and night transect data showed that balloonfish were unevenly distributed by size class across and within the four zones (Fig. 1). Small balloonfish were found more than expected in mangrove, while large and medium fish were found less. In contrast, large and medium fish were found

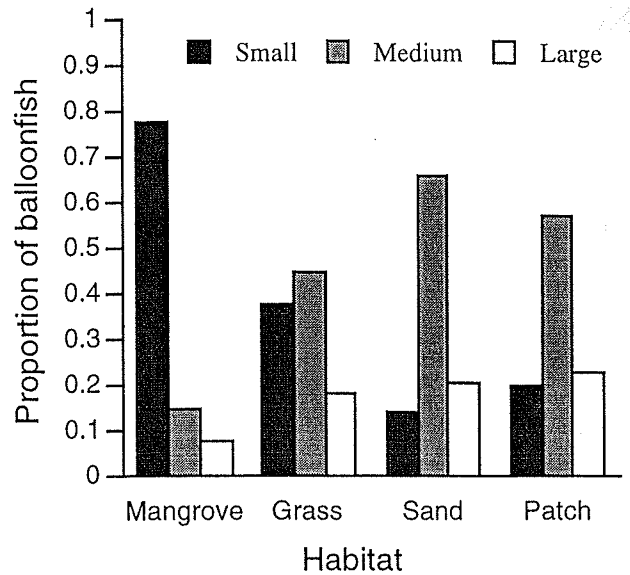

Figure 1. Proportion of balloonfish found in three size classes across four reef zones in Discover Bay, Jamaica. Data represent pooled day and night surveys.

more than expected in patch reefs while small fish were found less. All other findings were close to their expected values ($X^2 = 101.13$, df = 6, $p < 0.001$).

The interaction effect of time of day and reef zone on fish abundance varied across different reef zones ($F_{3,15} = 9.94$, $p < 0.001$, Fig. 2). Linear, orthogonal contrasts demonstrated that fish abundances did not differ between day and night in grass or sand ($p > 0.50$). However, balloonfish were more abundant in the mangrove during the day than night and more abundant in the patch reef at night than day ($p = 0.002$ and $p < 0.001$ respectively). Individual balloonfish spent a higher proportion of their time active during the night than day (Wilcoxon Chi-square = 3.5, $p < 0.001$, Fig. 3). During surveys, a greater frequency of fish was found at rest during the day than at night, whereas a greater frequency of fish was found active at night than during the day ($G = 349.16$, df = 1, $p < 0.001$; Fig. 4).

All mangrove balloonfish were observed by day to aggregate at the top of the water column in non-interacting groups of 5-10 small individuals. At night, however, man-

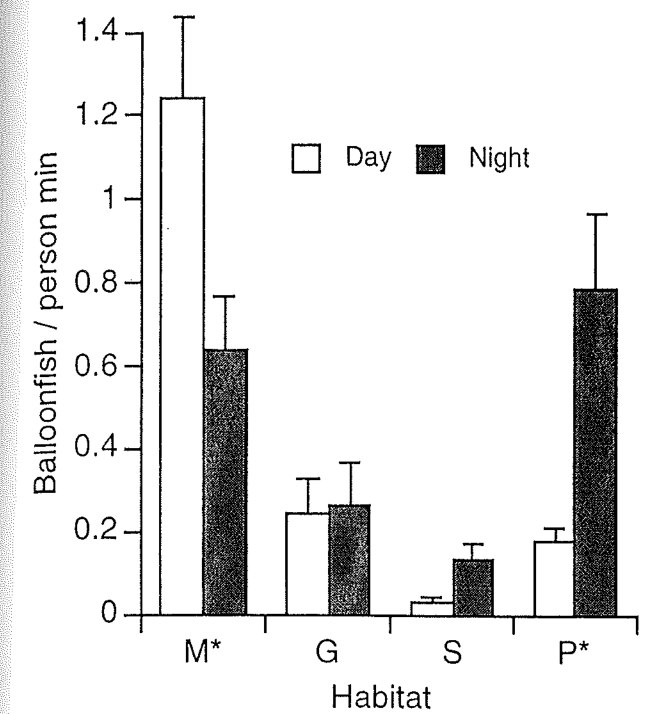

Figure 2. Mean number (±SE) of balloonfish found per person min in mangrove, grass, sand, and patch reef zones compared between day and night surveys (n = 3). Asterix indicates signigicant differences in balloonfish abundance between day and night (P < 0.05), based upon linear orthogonal contrasts.

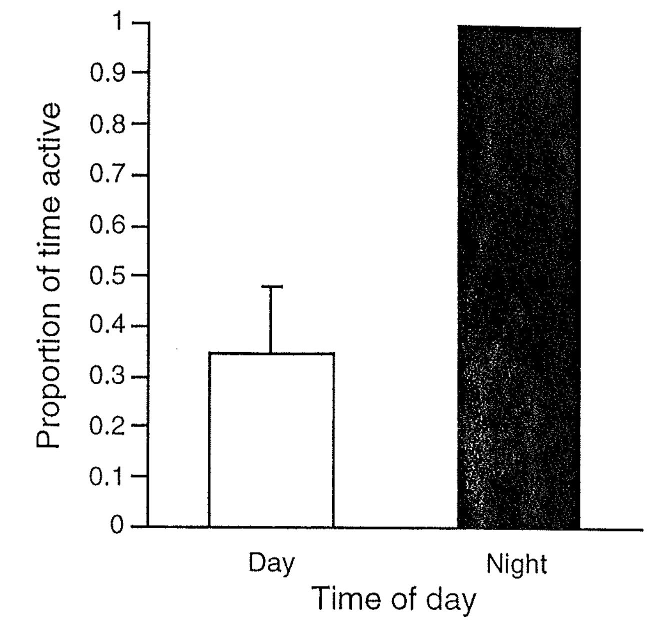

Figure 3. Proportion of time balloonfish spent active in day vs. night across all reef zones in Discovery Bay, Jamaica during individual fish observations (n = 11 and 9 fish for day and night, respectively).

grove balloonfish were generally found lower in the water column, and a few were found foraging alone, beyond the mangrove roots. All of the small and medium mangrove balloonfish had predominantly rust-colored dorsal surfaces, while small and medium back reef balloonfish had mostly beige dorsal surfaces.

Discussion

Balloonfish distribution varied across reef zones in Discovery Bay. Balloonfish seemed to prefer patch reef and the mangroves over sand and grass, possibly because these latter two habitats do not provide adequate food or shelter for balloonfish. Within the preferred zones, balloonfish were further segregated according to size class. The mangrove, where small balloonfish were most abundant, offers calm water and numerous protective roots and crevices. Smaller fish, which may be more susceptible to predation and rough waves than large fish, may seek refuge in the mangrove. Large fish, at less risk of predation, may be able capitalize on a potentially greater availability of food in patch reef habitat. Future studies should track balloonfish cohorts in order to document possible habitat change with increasing fish size.

Many balloonfish seem to be nocturnal. Activity, as quantified both by proportion of time individuals spent swimming and foraging and by the number of swimming fish encountered during surveys, was higher at night throughout the reef. In the patch reef, the most preferred zone for large fish, balloonfish abundance was higher at night then during the day. Predation pressure may drive balloonfish behavior. On the back reef by day, most resting balloonfish were well hidden in crevices or beneath grass. Daytime concealment may decrease the chances of detection by visual predators.

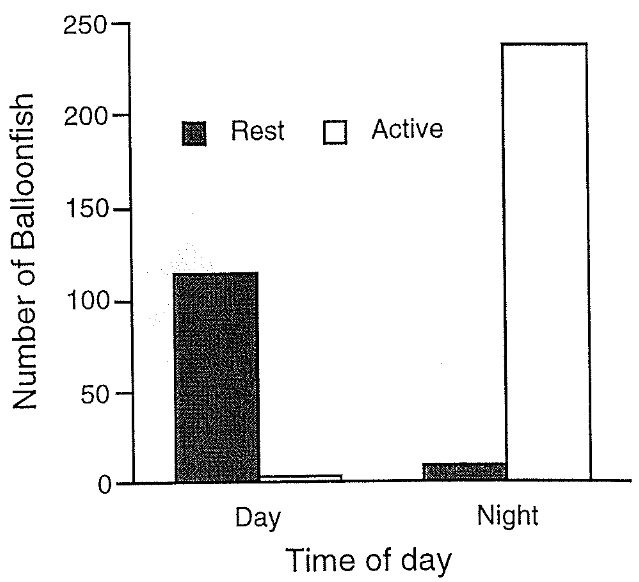

Figure 4. Effect of time of day on balloonfish activity level from survey results over day and night (n = 3) across all reef zones in Discover Bay, Jamaica.

Balloonfish spines and their ability to rapidly increase in size may however, be adequate defense against most predation. If this is the case, predator avoidance would not be the primary mechanism driving balloonfish activity patterns. One alternative is that balloonfish are more active at night due to increased prey availability. A large proportion of their diet consists of nocturnal crustaceans, mollusks, and echinoderms (Thresher 1980). Future research examining predation rates and diel resource distribution could help establish the relative roles of predation and resource abundance in determining balloonfish behavior.

Our results suggest that the mangroves may be a refuge for small balloonfish. Selection pressures determining balloonfish behavior may be different in the mangrove than on the main backreef. This is suggested by the higher abundance of small balloonfish within the mangrove during the day as compared to night (the exact reverse of the pattern found in the patch reef), and the overall high levels of activity in this zone during day and night (personal observation). Low predation risk and food that is available to foragers during the day (food other than echinoderms, mollusks, and crustaceans) may interact to create an environment in which balloonfish are able to increase their daytime activity. In support of this idea, we observed several small balloonfish foraging off of the mangrove roots and rocks. Under cover of night, however, balloonfish may leave the mangrove to forage on prey that is only nocturnally accessible and more abundant in other reef habitats. This possibility may explain the decreased abundance of balloonfish in the mangrove by night. Alternatively, the relatively high abundance of balloonfish in the mangrove during the day may be explained by the small size of the refuge. The mangrove may not be able to nourish as many fish as it can shelter. Thus, fewer balloonfish were observed in the mangrove at night (peak foraging time on the main backreef) than during the day (peak hiding time).

The nocturnal niche displayed by many balloonfish differs from those of most fish species at Discovery Bay (Nagy et al. 2000), and in particular that of the related surgeonfish (family: Acanthuridae; Thresher, 1980). In contrast to balloonfish, surgeonfish are diurnal foragers whose streamlined bodies allow for speedy predator escape. Release from competition by switching to night foraging (niche diversification) or escape from diurnal predators could have driven balloonfish to occupy their current niche and evolve their present body form (both of which differ extremely from those of surgeonfish). Detailed investigations such as this one, describing the temporal and spatial aspects of niches may be useful in exploring mechanisms underlying high fish diversity on coral reefs.

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